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Digesting in hypoxia: impact on gastric evacuation rate and postprandial metabolism (SDA) of Atlantic cod, *Gadus morhua*

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Summary
Chronic hypoxia reduces both food consumption and growth rate of fish. As digestion results in increased oxygen uptake, the so-called specific dynamic action (SDA), a possible mechanism is that the reduction of aerobic metabolic scope imposed by hypoxia limits the increase in oxygen uptake during hypoxia. This in turn prolongs the SDA response and, conversely, decreases ingestion rate over time. However, nothing is known of the underlying processes in the stomach and the gut. This study investigates gastric evacuation (GE) rates at 3 levels of dissolved oxygen (90, 55 and 40% sat.) and the SDA response in normoxia and hypoxia (40 % sat.). GE proceeded significantly slower at 55 and 40% sat. compared with normoxia, and, as digestion proceeded, the moisture content of the bolus increased more slowly at 55 and 40% sat. than in normoxia. Further analysis of the available SDA data will reveal to what extent these support the suppressing effects of hypoxia on gastric performance.

Introduction
Like other marine fish exposed to low levels of dissolved oxygen (DO) or hypoxia, Atlantic cod, *Gadus morhua*, grow more slowly and eat less food (Chabot and Dutil 1999), and its growth and food consumption rates become proportional to DO below 70% sat. The main mechanism for this reduction in food consumption and growth rate is thought to be the reduction in aerobic scope (AS; maximum metabolic rate minus standard metabolic rate) in hypoxia, AS being a measure of energy available for e.g. activity, reproduction and food processing (Fry 1971), the latter being called the specific dynamic action (SDA, see Secor 2009). Low DO has been shown to reduce the amplitude of SDA and increase its duration (Jordan and Steffensen 2007). This study aims to assess the impacts of reduced DO on processes taking place in the stomach and in the gut by comparing the rate of gastric evacuation (GE) and the SDA of cod exposed to normoxia and hypoxia.

Materials and Methods
Adult cod were fed smelt (*Osmerus mordax*, ration of 4% body mass, range 3.5–4.5) at 6 °C. After feeding, DO was either kept at > 90% (N = 55) or rapidly dropped to 55 (N=45) or 40% sat. (N=48). Fish were randomly selected for determination of stomach content mass by gastric lavage at predetermined postprandial times (Figure 1). Gastric lavage proceeded as in Couturier et al. (2013). Cod of similar size were fed smelt at the same ration and their SDA measured twice, in normoxia and at 40% sat. The GE rate parameter of the square root model was estimated for each DO level following the procedure by Andersen (2012) and accounting for the variability of temperature, predator length and meal mass. Data for the first 12 h after feeding were excluded because the mass of the stomach content was abnormally elevated in normoxia compared with previous experiments of this type (Andersen, 2012). Data were truncated at the time of first occurrence of an empty stomach (Olson and Mullen, 1986). The determination of oxygen consumption and of SDA followed the methods of Chabot et al. (In press).

Results and Discussion
GE proceeded significantly more slowly at 55 and especially at 40% sat. compared with normoxia (Figure 1). As a consequence of this slower GE, the increased in moisture content of the bolus also proceeded more slowly in hypoxia than in normoxia (Figure 2). Although the slowing of GE was significant, it was less pronounced than the increase of SDA duration reported by Jordan and Steffensen (2007), but the conditions were different (10 °C, 5% ration, 30% sat.). Our own SDA results,
when available, will make the comparison of GE and SDA possible. Decreased GE, food consumption
and growth rates are expected to affect many coastal fish populations as the expansion of hypoxic
zones that started with industrialisation is expected to continue as climate warms due do increased
CO₂ emissions.

![Figure 1](image1.png)

Figure 1. The course of gastric evacuation of smelt prey fed to Atlantic cod at three DO levels: (a) normoxia, (b) 55% sat. and (c) 40% sat. Black filled symbols were used to fit the GE model. Open symbols were excluded because of abnormally high values within the first 12 h of digestion in normoxia. Filled grey symbols were excluded because of occurrence of empty stomachs at these sampling times.

![Figure 2](image2.png)

Figure 2. The course of moisture content of smelt prey fed to Atlantic cod at three DO levels: (a) normoxia, (b) 55% sat. and (c) 40% sat. Symbols as in Figure 1, except for crosses in normoxia, which were considered outliers and excluded from the regression.

References